On some particular sclerotized structures associated with the vulvar area and the vestibulum in Orthotylinae and Phylinae (Heteroptera, Miridae)[1]

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Abstract: A review of the literature on mirid female genitalia, combined with new observations, shows that asymmetrical sclerotized structures occur in four tribes belonging to two mirid subfamilies: Orthotylinae Orthotylini, and Phylinae Hallodapini, Leucophotopterini, Phylini. The structures are adjacent to the vulva (Orthotylinae) and the vestibulum (Phylinae). In the latter case, the sclerotized structures are directed towards the right side. In Orthotylinae, the vulvar area may be surrounded by complicated plates or lobes originating from the internal margin of the anterior gonapophyses (first valvulae). In Phylinae, the vestibulum may be strongly modified by sclerotization of some or most parts of its wall; in some Hallodapini (if not all), the sclerotized vestibulum bears a vesicular sac-like diverticulum. The sclerotized structures appear highly adaptive and related to the structure of the vesica (in Phylinae), of the parameres and probably also to the various spiculi of the conjunctiva (in Orthotylinae). Within Phylinae, size and shape of the sclerotized part of the vestibulum are closely correlated to size and shape of the vesica; thus, like the vesica, the vestibulum may be either short and relatively straight or C- or S-shaped, twisted with a complete loop, or not. In some cases, the vestibulum is modified into a highly specialized organ acting as a reinforced copulatory duct. The hypothesized functions of these documented sclerotized structures are: defence system for the female against potentially wounding by the male organ; a strengthening device for coupling, guidance and support of the vesica.

Key words: adaptive trend, copulatory duct, female genitalia, gonapophyses, Heteroptera, Miridae, Orthotylinae, Phylinae, vestibulum, vulva.

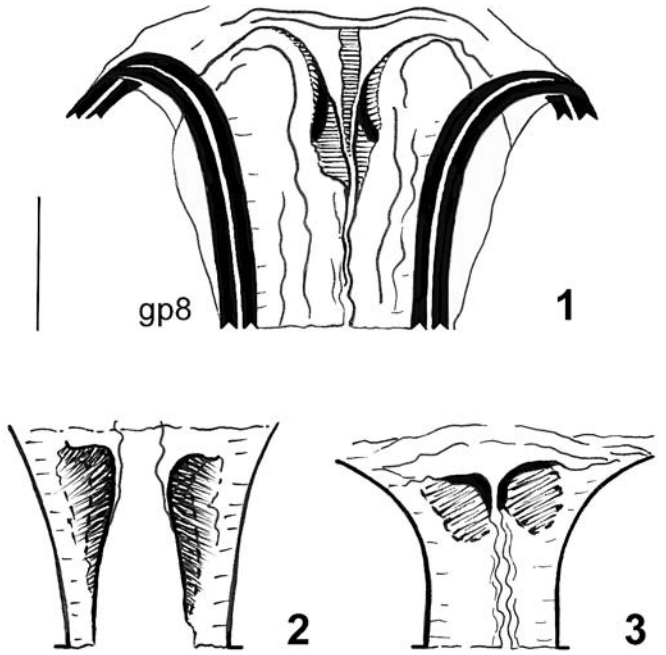
Introduction

A specific structure was recently discovered in the floor of the vagina of a new orthotyline species of *Cyllecoris* (*C. ernsti* Matocq & Pluot-Sigwalt 2006): an asymmetrical stout tube-like body strongly sclerotized and pigmented, directed toward the right side and located below the ring sclerites near the vulvar area. This discovery led us to survey the literature dealing with female genitalia in Miridae to determine if other species possess comparable morphology, or to find some data allowing to shed light on this enigmatic female genital structure.

Such genital differentiation has never been described elsewhere in the Orthotylinae. In several major contributions involving various orthotyline species, no particular structure is mentioned: Kullenberg (1947) in *Cyllecoris* [*histrionius* (L.)], *Dryophilocoris*, *Orthotylus*, *Heterotoma*; Slater (1950) in various orthotyline species; Davis (1955) in *Lopidea*; Southwood (1953), Scudder (1959), and Ehanno (1990a) in *Orthotylus*. However, several of these authors noticed some asymmetrical organization of the vulvar area or unusual sclerotized protuberance in this region (see Kullenberg, Davis, Ehanno, loc. cit.). More recently, Gagné (1997) in *Nesiomiris* and Schwartz (2004)

[1]We are very pleased to dedicate this paper to our colleague and friend Ernst Heiss on the occasion of his 70th birthday.

Denisia 19, zugleich Kataloge der OÖ. Landesmuseen Neue Serie 50 (2006), 557–570



Figs 1-3: Orthotylinae Halticini, sclerotized areas observed between the gonapophyses 8 (gp8) at the level of the vulva; ventral view; (**1**) *Halticus luteicollis*; (**2**) *Pachytomella parallela*; (**3**) *Dimorphocoris* sp. Scale bar = 0.1 mm.

in *Melymacra* mentioned and illustrated strongly convoluted plates between the first valvulae.

In the Phylinae, however, several authors have described curious vaginal structures, as a curved sclerotized duct, lateral "tube", or "ventral sac", that should be analogous, if not homologous, to the structure described in *Cyllecoris*: in the Phylini (SCHMITZ 1976; HENRY & SCHUH 1979; SCHUH 1984; EYLES & SCHUH 2003), as well as in the Hallodapini (EHANNO 1990b; MAGNIEN 2000; WYNIGER 2006). Asymmetry is also often pointed out. In several species, EYLES & SCHUH (2003) suggest that the sclerotized structures might be a guide and support for the long and looped phallus.

In the literature of female genitalia, most authors have focused on the vagina in dorsal view (roof of the genital chamber and ring sclerites), and the posterior wall (mainly K-structures). Morphological data concerning other structures of the genitalia, in particular the vulvar area and the floor of the vagina, are scarce and dispersed. In this paper, we attempt to summarize knowledge of the particular sclerotized structures found in these areas, bringing together information from the literature and original observations of several previously unexamined species. This study provides a basis for further research and draws attentions to genital regions still poorly known.

Material and Methods

Species examined: These were selected from subfamilies Orthotylinae and Phylinae to confirm or add precision to literature data, and for comparison purpose. Hereinafter we follow the classification proposed by SCHUH (1995). About thirty species were examined, as follow:

Orthotylinae. – Halticini: *Dimorphocoris* sp., *Halticus luteicollis* (PANZER 1804), *Pachytomella parallela* (MEYER-DÜR 1841). – Orthotylini: *Cyllecoris ernsti* MATOCQ & PLUOT-SIGWALT 2006, *C. histrionius* (LINNAEUS 1767), *Dryophilocoris luteus* (HERRICH-SCHAEFFER 1835), *Mecomma ambulans ambulans* (FALLÉN 1807), *Orthotylus marginalis* REUTER 1883.

Phylinae. – Hallodapini: *Cremnocephalus alpestris* WAGNER 1941, *C. matocqi* MAGNIEN 2000. – Phylini: *Amblytylus brevicollis* FIEBER 1858, *A. nasutus* (KIRSCHBAUM 1856), *Anomalocornis peyreti* COSTA & COUTURIER 2002, *Atractotomus magnicornis* (FALLÉN 1807), *A. mali* (MEYER-DÜR 1843), *A. kolenatii* (FLOR 1860), *Campylomma annulicorne* (SIGNORET 1865), *Criocoris sulcicornis* (KIRSCHBAUM 1856), *Dasycapsus theryi* POPPIUS 1912, *Heterocapillus tigripes* (MULSANT & REY 1852), *Lopus decolor* (FALLÉN 1807), *Megalocoleus molliculus* (FALLÉN 1807), *M. longirostris* (FIEBER 1807), *Phoenicocoris dissimilis* (REUTER 1878), *Plagiognathus arbustorum arbustorum* (FABRICIUS 1794), *Psallus perrisi* (MULSANT & REY 1852), *Tuponia macedonica* WAGNER 1957.

Three tribes have not been investigated: Nichomachini in Orthotylinae; Leucophoropterini and Pilophorini in Phylinae.

Dissection, examination: Females are dissected after KOH treatment following the recommendations of EHANNO (1990a). The genitalia are first examined entire under a microscope, without coloration. Thereafter, it is necessary to remove the gonapophyses 9 (second valvulae) and the posterior wall if necessary, in order to see the vulvar area clearly at the base of the gonapophyses 8 (first valvulae), the vestibulum and the floor of the vagina. The genitalia are then slightly stained with chlorazol black and examined again; further dissection is performed if necessary. The genital

parts studied are best observed in ventral and caudal views. All illustrations were made from temporary slide mounts in lactophenol.

Terminology: The terminology of the genital structures follows DUPUIS (1970) and EHANNO (1990a).

Results

Localization and inventory of the structures

The literature survey showed that unusual features associated with the floor of the vagina occur in certain tribes of at least two mirid subfamilies, the Orthotylinae (Orthotylini: Table 1) and the Phylinae (Hallodapini, Leucophoropterini and Phylini: Table 2). As far as we know, comparable features do not seem to occur in Orthotylinae Halticini or in other mirid groups; see for instance comparative studies concerning several Mirinae (FONTES 1981, 1989, 1992a, 1992b; ROSENZWEIG 1997; SCHWARTZ & FOOTTIT 1998) or the study of EHANNO (1989) about *Deraeocoris* (Deraeocorinae). Nevertheless unpublished data obtained by F. Chérot (pers. comm.) strongly suggest that unusual features may occur in these subfamilies, and in others as well.

The features discussed in the present paper are mainly asymmetrical sclerotized structures, often duct-like and directed to the right side (to the left side in all Figures, the structures being represented in ventral view). They are located in two adjacent regions, the vulvar area in Orthotylinae and the vestibulum sensu DAVIS (1955) in Phylinae. Both are poorly known regions that are not easy to observe and morphologically complex.

– The vulva is delimited anteriorly by the subgenital plate, posteriorly by the base of the ovipositor. Sclerotized structures are observed between the gonapophyses 8 (first valvulae), on the internal margin of the curved region.

– The vestibulum is the short, narrow, passage extending from the vulva to the vagina (genital chamber). It has been recognized by DAVIS (1955) as different from the vulvar opening and thus rightly named to distinguish it clearly. It appears as part of the floor of the vagina (just below the ring sclerites and the vermiform gland). It is often connected to the sclerites linking the fibulae and the gonapophyses 8.

Tables 1 and 2 list all such structures in the vulvar area and the vestibulum. In the literature, they are usually very succinctly described, sometimes only illustrated without comment. When pigmented (brownish-yellow to brown) and sclerotized, they are obvious, and clearly visible through the membranous dorsal wall of the vagina. When unpigmented, they are inconspicuous and usually pass unnoticed.

1) Miridae: Orthotylinae (Table 1)

Halticini. No particular structure has been described in this tribe, except some apparently common microsclerites or small sclerotized areas more or less distinctly delimited in the vulvar area between the gonapophyses 8 (CHÉROT et al. 2004) (Figs 1-3). Asymmetry was not observed. The floor of the vagina may have slightly sclerotized areas as described by EHANNO (1990c, 1991, 1992). The vestibulum is not distinct, being apparently not (or weakly) sclerotized and unpigmented.

Orthotylini. Various structures have been described within Orthotylini, particularly in the vulvar area: from simple to highly complex, symmetrical or slightly to strongly asymmetrical. In all the species studied, the vestibulum – probably short and membranous – is not distinct.

After KULLENBERG (1947) who mentioned the presence of sclerotized parts around vulvar area, DAVIS (1955) and EHANNO (1990a) described respectively in *Lopidea* and *Orthotylus* lateral lobes or bulbous protuberances converging medially to form an asymmetrical structure which extends ventrally into the vestibulum. Similar lobes, erroneously considered as glandular, have also been illustrated in several species of *Rolstonocoris* by SCHAFFNER & FERREIRA (1997).

As shown by Figs 4-6, these lobes or plates, which can all be regarded as a thickened extension of the internal margin of the gonapophyses 8, appear rather different

Table 1: Particular structures observed (described or figured) ventrally in female genitalia of some Orthotylinae in vulvar area, vestibulum or vaginal floor; literature and original data. Abbreviation: gp8, gonapophyses 8 (first valvulae).

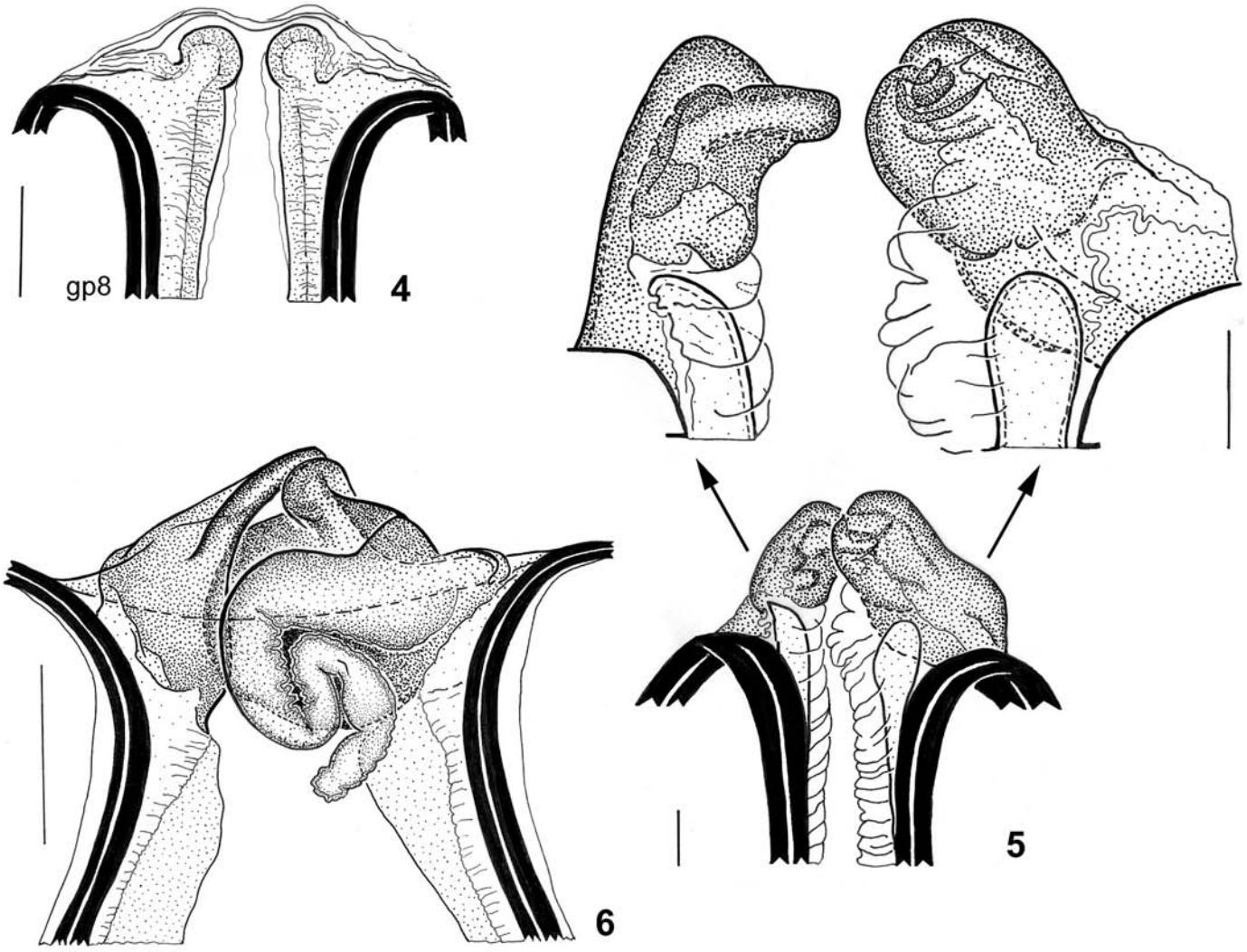
Taxa	Features or structures mentioned	Authors
Halticini		
Coridromius	Three sclerites between gp8	Chérot et al. 2004
Dimorphocoris	Sclerotized area on the vaginal floor	Ehanno 1992
—-	Pair of symmetrical microsclerites in areas weakly sclerotized between gp8 (Fig. 3)	Present paper
Halticus	Pair of symmetrical microsclerites in areas weakly sclerotized between gp8 (Fig. 1)	Present paper
Myrmecophyes	Symmetrical microsclerites in the vulvar area	Schuh & Lattin 1980
——	Sclerotized area on the vaginal floor	Ehanno 1990c, 1991
Pachytomella	Two small symmetrical sclerotized areas between gp8 (Fig. 2)	Present paper
Orthotylini		
Ceratocapsus	[From illustrations] Various asymmetrical sclerotized structures depicted below the ring sclerites]	Carvalho et al. 1983
Cyllecoris (*histrionius*)	Asymmetrical vulva	Kullenberg 1947
——	Irregular sclerotized plates on each side of the vulva (Fig. 6)	Present paper
(*ernsti*)	Idem + tube-like structure on vulvar area or vestibulum	Matocq & Pluot-Sigwalt 2006
Dryophylocoris (as *Cyllecoris*)	Vulva surrounded by sclerotized formation arched upwards	Kullenberg 1947
——	Sclerotized and convoluted plates at base of gp8	Present paper
Globiceps	Sclerotized area on the vaginal floor	Ehanno 1990a
Heterotoma	Sclerotized area on the vaginal floor	Ehanno 1990a
Lopidea	Asymmetrical sclerotized protuberance ventrally into vestibulum	Davis 1955
Mecomma	Pair of plates almost symmetrical at base of gp8 (Fig. 4)	Present paper
Melymacra	Base of gp8 and adjacent vestibulum strongly convoluted	Schwartz 2004
Nesiomiris	Sclerotized "pocket" anterior to bases of gp8	Gagné 1997
Orthotylus	Asymmetrical vulva; sclerotized plates at base of gp8	Kullenberg 1947
——	Asymmetrical sclerotized bulges at base of gp8	Ehanno 1990a
——	Pair of sclerotized sinuous plates at base of gp8 (Fig. 5)	Present paper
Rolstonocoris	Sinuous plates at base of gp8 considered as glandular	Schaffner & Ferreira 1997

from one genus to another and to a lesser extent between species (see also Gagné 1997; Schwartz 2004). They may be poorly developed, regular and almost symmetrical (Fig. 4), or well-developed, highly irregular and even contorted, strongly asymmetrical (Fig. 5). In this case, they are thick, their surfaces (upper and lower) being not plane, but with bumps, holes, and grooves. Apparently, these plates might be more or less overlapped at rest. In some species as *Cyllecoris ernsti*, the extension may give rise to a strong sclerotized tube-like differentiation (Matocq & Pluot-Sigwalt 2006) directed to the right side. One can remark that the tube-like structure described in *C. ernsti* seems also present in *C. histrionius* (Fig. 6), although not exactly at the same place, more posteriorly and not pigmented.

Obviously, asymmetrical vulvar plates as well as a likely complicated vaginal floor seem to exist also in *Ceratocapsus* as shown by the drawings of the female genitalia in 16 species studied by Carvalho et al. (1983). Among the various conspicuous formations drawn, some appear as tube-like structures strongly sclerotized.

2) Miridae: Phylinae (Table 2)

Hallodapini. The presence of a large "ventral sac" has been reported in several genera (*Alloeomimus*, *Cremnocephalus*, *Hallodapus*, *Mimocoris*, *Omphalonotus*, *Systellonotus*) by Ehanno (1990b), Magnien (2000) and Wyniger (2006) who gave several illustrations. According to Magnien (loc. cit.), the size of the sac varies between species (see also Wyniger loc. cit.) and is related to the size of the vesica (see Discussion).



Figs 4-6: Orthotylinae Orthotylini, sclerotized plates and lobes differentiated on the internal margin of the gonapophyses 8 (gp8) on each side of the vulva; ventral view; (**4**) *Mecomma ambulans*; (**5**) *Orthotylus marginalis*, general view and details (**6**) *Cyllecoris histrionius*. Scale bars = 0.1 mm.

As observed by us in two *Cremnocephalus* species, the ventral sac is a vesicular diverticle arising from the anterior part of the vestibulum (Figs 7-10). Near the vulva, the vestibulum is first an apparently convoluted duct lighly sclerotized with indistinct lumen; it soon turns abruptly towards the right side, then to the left, before expanding into a wide flat vesicular sac. The cuticular wall of this diverticulum is thin and relatively rigid, uniformly weakly sclerotized, pale yellow pigmented. The whole sac is closed anteriorly and free, only connected at its base: ventrally to the vestibulum, dorsally to the vaginal wall. The latter connection is realized through a short membranous passage not easy to observe, near the junction of the genital chamber and the seminal sac.

The vulvar area itself lacks notable features (except a pair of microsclerites) and is almost symmetrical. However it will be necessary to examine additional species before reaching conclusions. The two microsclerites described and figured by SCHMITZ (1969) in *Kapoecius* are strongly asymmetrical and sclerotized; they look more like what is observed in the Orthotylini.

Leucophoropterini. We have not been able to examine a representative of this tribe. From the little available data found in the literature (Table 2), it seems that there is only a pair of microsclerites, or a pair of small sclerotized areas well delimited. Nevertheless, EYLES & SCHUH (2003) have described in *Sejanus* a curved lightly sclerotized structure below the ventral labiate plate which could be a modified part of the vestibulum.

Phylini. Several structures showing varying degrees of complexity, from very simple to highly complex, have been described or

Table 2: Particular structures observed (described or figured) ventrally in female genitalia of some Phylinae in vulvar area, vestibulum or vaginal floor; literature and original data. Abbreviation: gp8, gonapophyse 8 (first valvulae).

Taxa	Features or structures mentioned	Authors
Hallodapini		
Alloeomimus	Ventral sac	Magnien 2000
Cremnocephalus	Ventral sac	Ehanno 1990b
——	Sac-like structure	Magnien 2000
——	Ventralsack	Wyniger 2006
——	Vestibulum S-shaped, bearing a vesicular diverticulum (Figs 7-10)	Present paper
Hallodapus	Ventral sac	Ehanno 1990b
——	Ventral sack	Wyniger 2006
Kapoecius	Pair of asymmetrical irregular sclerites at base of gp8	Schmitz 1969
Mimocoris	Ventral sac	Ehanno 1990b
——	Sac-like diverticulum more or less elongated	Magnien 2000
——	Ventral sack	Wyniger 2006
Omphalonotus	Ventral sac	Ehanno 1990b
——	Ventral sack	Wyniger 2006
Systellonotus	Ventral sack	Wyniger 2006
Leucophoropterini		
Sejanus	Curved structure lightly sclerotized	Eyles & Schuh 2003
Tytthus	Two small fusiform plates	Schmitz 1976
——	Sclerotized triangles	Eyles & Schuh 2003
Phylini		
Agrametra	Two S-shaped folds more or less sclerotized and juxtaposed	Schmitz 1976
Amblytylus	Curved vestibulum comprising a C-shaped sclerotized part	Present paper
Anomalocornis	Sclerotized structure on the vaginal floor	Costa & Couturier pers. comm.
——	Duct-like vestibulum, S-shaped with complete loop (Figs 11, 12, 20)	Present paper
Atractotomus (as *Psallus*)	Unpaired sclerotized plate on the floor	Matocq & Péricart 1986
——	Vestibulum sinuous, rounded apically (Figs 13, 14)	Present paper
Basileobius	Triangular flexible pouch	Eyles & Schuh 2003
Beamerella	Asymmetrical "lateral tube" arising from vulvar area	Henry & Schuh 1979
Campylomma	Sclerotized structure heavily curved	Eyles & Schuh 2003
——	Curved vestibulum comprising a C-shaped sclerotized part	Present paper
Chlamydatus	Sclerotized plates laterally on the vulva	Kullenberg 1947
Criocoris	Vestibulum straight, unsclerotized, almost symmetrical (Fig. 15)	Present paper
Coatonocapsus	Lateral "tube"	Henry & Schuh 1979
Cyrtodiridius	Curled plate with wider apical head	Eyles & Schuh 2003
Dasycapsus	Vestibulum straight, unsclerotized, almost symmetrical	Present paper
Halormus	Flattened sclerotized duct	Eyles & Schuh 2003
Hambletoniola	Asymmetrical "lateral tube" arising from vulvar area	Henry & Schuh 1979
Helenocoris	Two sclerites almost symmetrical; S-shaped fold making a sclerotized roll	Schmitz 1976
Heterocapillus	Vestibulum mostly sclerotized, S-shaped (Fig. 17)	Present paper
Hirtopsallus	Two asymmetrical sclerites; S-shaped fold more or less sclerotized	Schmitz 1976
Insulopus	Two sclerites slightly asymmetrical	Schmitz 1976
Lopus	Curved triangular structure	Eyles & Schuh 2003
——	Curved vestibulum comprising a C-shaped sclerotized part	Present paper
Mecenopa	Curled "duct"	Eyles & Schuh 2003
Megalocoleus	Curved vestibulum comprising a C-shaped sclerotized part	Present paper
Neisopsallus	Two asymmetrical sclerites; S-shaped fold in vestibulum	Schmitz 1976
Odhiambolla	Asymmetrical "lateral tube" arising from vulvar area	Henry & Schuh 1979
Oligobiella	Two sclerites almost symmetrical; S-shaped fold in vestibulum	Schmitz 1976
Phoenicocoris	Vestibulum sclerotized and convoluted, S-shaped, asymmetrical	Schwartz & Stonedahl 2004
——	Vestibulum sclerotized and convoluted, S-shaped (Fig. 19)	Present paper

Taxa	Features or structures mentioned	Authors
Pimeleocoris	Vulva covered by a fold coming from the posterior wall	Eyles & Schuh 2003
Plagiognathus	Vulva covered by a fold coming from the posterior wall	Kullenberg 1947
——	Sclerotized asymmetrical protuberance into vestibulum	Davis 1955
——	S-shaped sclerotized fold along vestibulum (Fig. 18)	Present paper
Polyozus	Sclerotized structure	Eyles & Schuh 2003
Psallus	Curved vestibulum comprising a C-shaped part	Present paper
Rubrocuneocoris	Asymmetrical tube associated with right ring of bursa copulatrix	Schuh 1984
Tuponia	Vestibulum straight, unsclerotized, almost symmetrical (Fig. 16)	Present paper
Xiphoides (as "*Sthenarus*")	Lateral "tube" sclerotized	Henry & Schuh 1979
—— (as "*Sthenarus*")	Lateral "tube" well-developed	Schuh 1984
——	Prominent duct, sclerotized, curled	Eyles & Schuh 2003

figured in Phylini. Despite this diversity, a certain homogeneity does exist; the structures might not be so different as they seem at first sight and basically of the same type.

Several authors noticed symmetrical or asymmetrical microsclerites (most paired) at the base of the gonapophyses 8 (Schmitz 1969, 1976; Schuh & Lattin 1980; Eyles & Schuh 2003). These microsclerites, which seem widespread within Phylinae, and probably other subfamilies, originate from the internal margin of the gonapophyses and appear more or less well-delimited, and distinct between species.

More interesting are the tube-like structures already recorded in some genera (Henry & Schuh 1979; Schuh 1984; Eyles & Schuh 2003). They are unpaired structures often S-shaped at the level of the vestibulum. Because they are usually curved, sinuous, not in the same plane from base to apex, not regularly sclerotized all along the length, a given structure may differ in appearance (shape, size) in the same specimen when observed from different angles: as a tube or as groove, continuous or discontinuous, becoming distally narrower or broader.

In fact, within Phylinae, the vestibulum shows a wide range of shape and appearance. Three patterns can be recognized following the importance of the modifications observed.

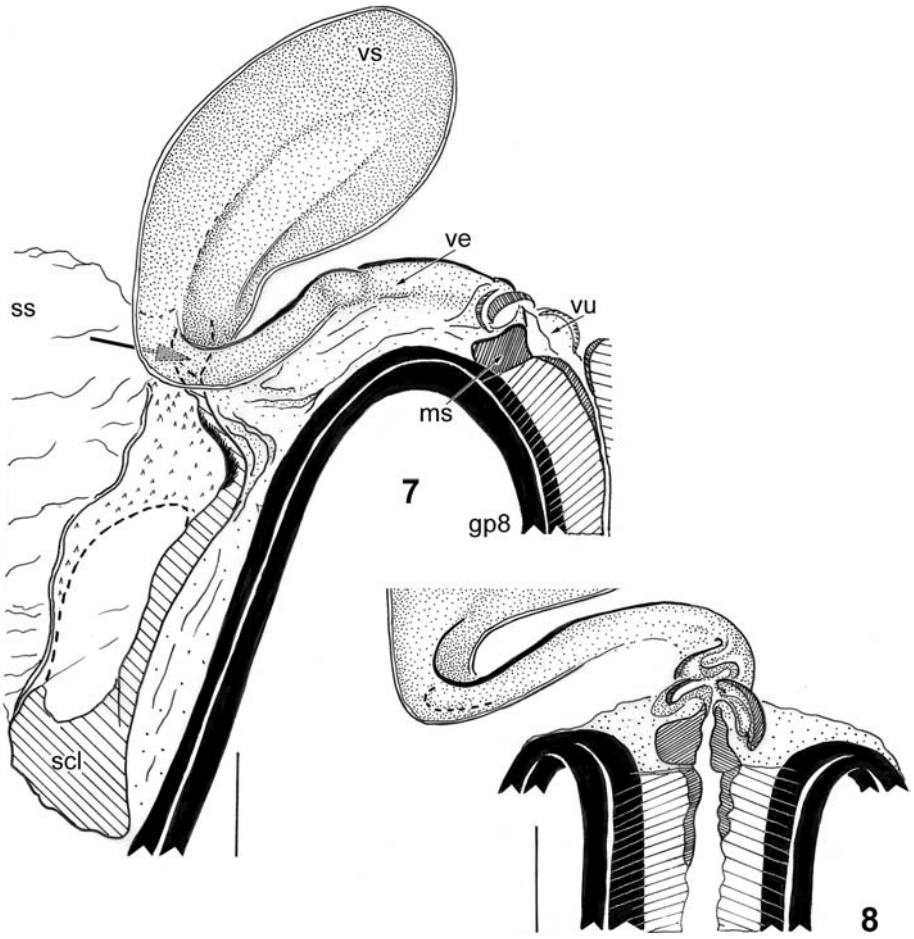
1. Vestibulum rather short and straight, without evident sclerotized part along its length (Fig. 15). The whole structure is relatively symmetrical, membranous although thick-walled, not strongly convoluted. Included species: *Criocoris*, *Dasycapsus*.

2. Vestibulum of moderate size, C-shaped, with sclerotized wall localized in the curve (Fig. 16). The vestibulum is clearly asymmetrical; the curve is well marked, directed towards the right side and it possesses at this level a sclerotized wall. The vulva itself, between the base of the gonapophyses 8, exhibits such usual features common microsclerites more or less well-delimited between the base of the gonapophyses 8. Included species: *Amblytylus*, *Campylomma*, *Lopus*, *Megalocoleus*, *Psallus*, *Tuponia*.

3. Vestibulum often conspicuous, S-shaped, mostly sclerotized (Figs 11-14, 17-20). The vestibulum appears to be a weakly pigmented twisted duct. The cuticular wall is relatively rigid except in the more basal part, rather membranous near the vulva. The size, the twist and turns are different and more or less pronounced following the studied species. Included species: *Anomalocornis*, *Atractotomus*, *Heterocapillus*, *Phoenicocoris*, *Plagiognathus*.

In pattern 2, the sclerotized part is localized to the curved section of the vestibulum. In pattern 3, the whole vestibulum seems often homogeneously sclerotized. However thickening of the wall, pigmentation and sclerotization are localized, always lengthways, mostly in the curves. The rest of the cuticular wall remains unsclerotized, unpigmented and flexible. The lumen, extremely narrow and convoluted, is usually indiscernible except in some places; its course cannot be followed.

The transition between the modified vestibulum and the vagina is indistinct and very hard to see. In every case where it has



Figs 7-8: Phylinae Hallodapini, sclerotized differentiation in the vulvar area and the vestibulum; the vestibulum is here modified into a highly specialized copulatory duct bearing a vesicular diverticulum (ventral sac); (**7**) *Cremnocephalus matocqi*, ventrolateral view; (**8**) idem, ventral view showing the vulvar area. gp8, gonapophyses 8; ms, microsclerite; ss, seminal sac; ve, vestibulum; scl, sclerite linking gonapophyses and fibulae; vs, ventral sac; vu, vulva; arrow indicates the connection between the vestibulum and the vagina under the ventral sac. Scale bars = 0.1 mm.

been properly observed (in *Cremnocephalus*, *Anomalocorinis*, *Phoenicocoris*, *Plagiognathus*), the transition was realized via a rather large membranous portion opening near the junction of the vagina (genital chamber) and the seminal sac (Figs 7, 19, 20, arrow).

Discussion

Perhaps because of their complexity and diversity the internal female genitalia of the Miridae are still poorly known. In this field, there is obviously a great need for comparative morphological investigations (CHÉROT 1996). The morphology and origin of the sclerotized genital structures described in this paper remain to a large extent inadequately understood. Dissections of dried female specimens only cannot clarify several aspects of the morphological structure, and many points will remain unresolved without additional histological studies. Thick sectioning could be used to examine the internal anatomy of the vulva and the vestibulum; in particular serial cross sections could help to discern some details more accurately (origin and relation of the various cuticular elements, junctures, lumen, possible musculature) as well as the overall organization and the topography of both areas.

Nevertheless, despite our limited understanding of the female genitalia in Miridae, and although literature data is difficult to use (due to its disparity and frequent imprecision), several general observations can be made.

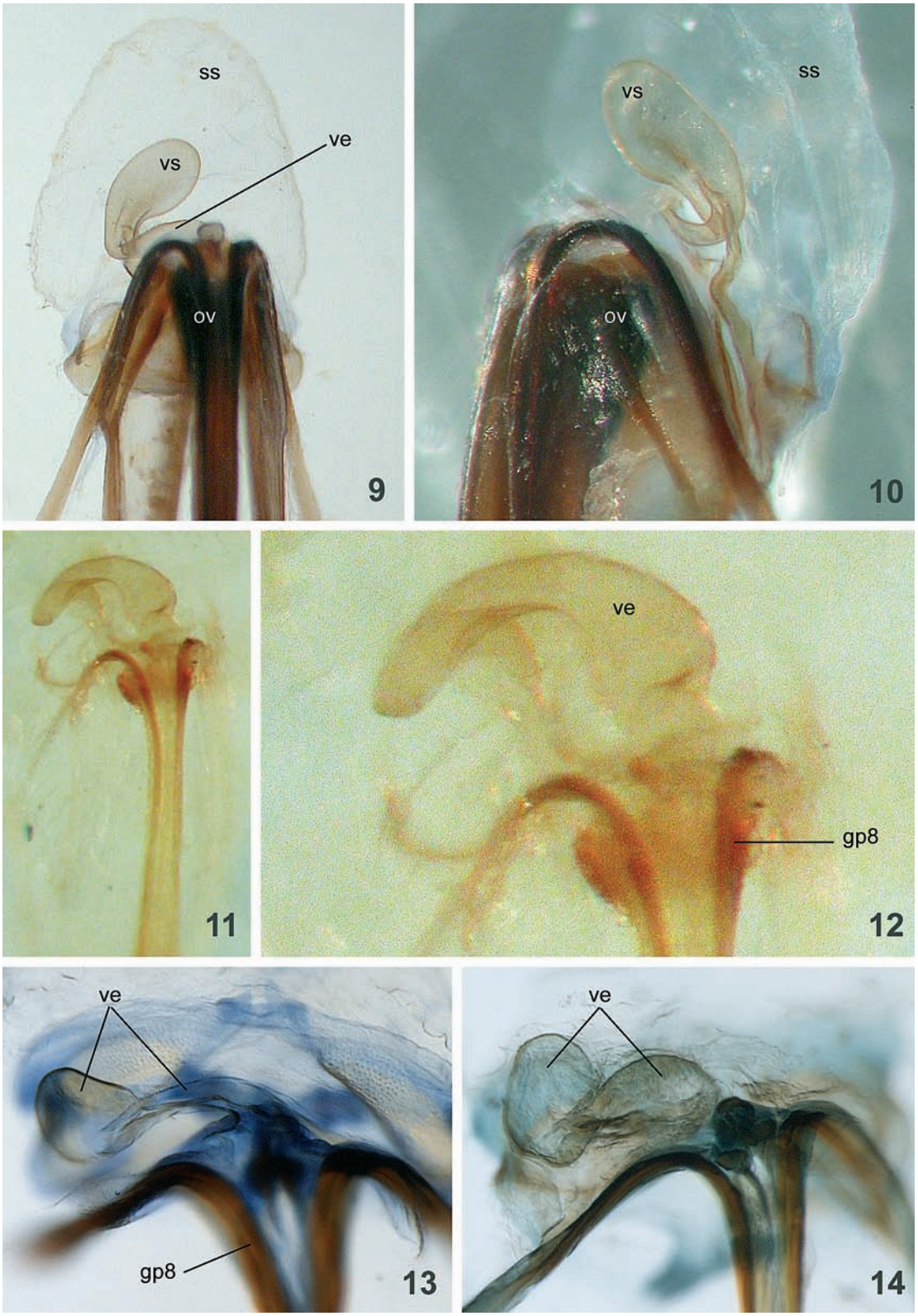
Are the sclerotized structures all homologous?

Within the Miridae, only two subfamilies, the Orthotylinae and the Phylinae, two closely related subfamilies having sister group relationships (SCHUH 1974, 1976), seem to have sclerotized differentiation adjacent to the vulva and vestibulum. Are the documented structures in these related groups homologous, or only more or less analogous for morpho-mechanical reasons or parallel tendencies?

It is certainly premature to answer this question. It is first necessary to examine all tribes in both subfamilies, with additional representatives of each, in order to obtain an adequate appraisal of the importance and origin of the structures. It will be also necessary to adequately investigate the other subfamilies of Miridae. Obviously there exists in Phylinae and Orthotylinae a similar tendency towards complexity in the vulvar area and the vestibulum, as well as a tendency to develop sclerotized structures. Initially, even considering the similar sclerotized ducts, these structures seem to be fundamentally different in the two subfamilies.

Globally, the cuticular differentiation affects two adjacent areas. It seems that within Orthotylinae the differentiations more particularly involve the vulva (i.e. the internal margin of the gonapophyses 8), whereas in the Phylinae the vestibulum is more heavily modified than the vulva.

Unfortunately in Orthotylinae, the Orthotylini condition remains unclear and for that reason the structures described cannot easily be compared with those described for the Phylinae. Our understanding of the structure in the Phylinae are clearer: all the

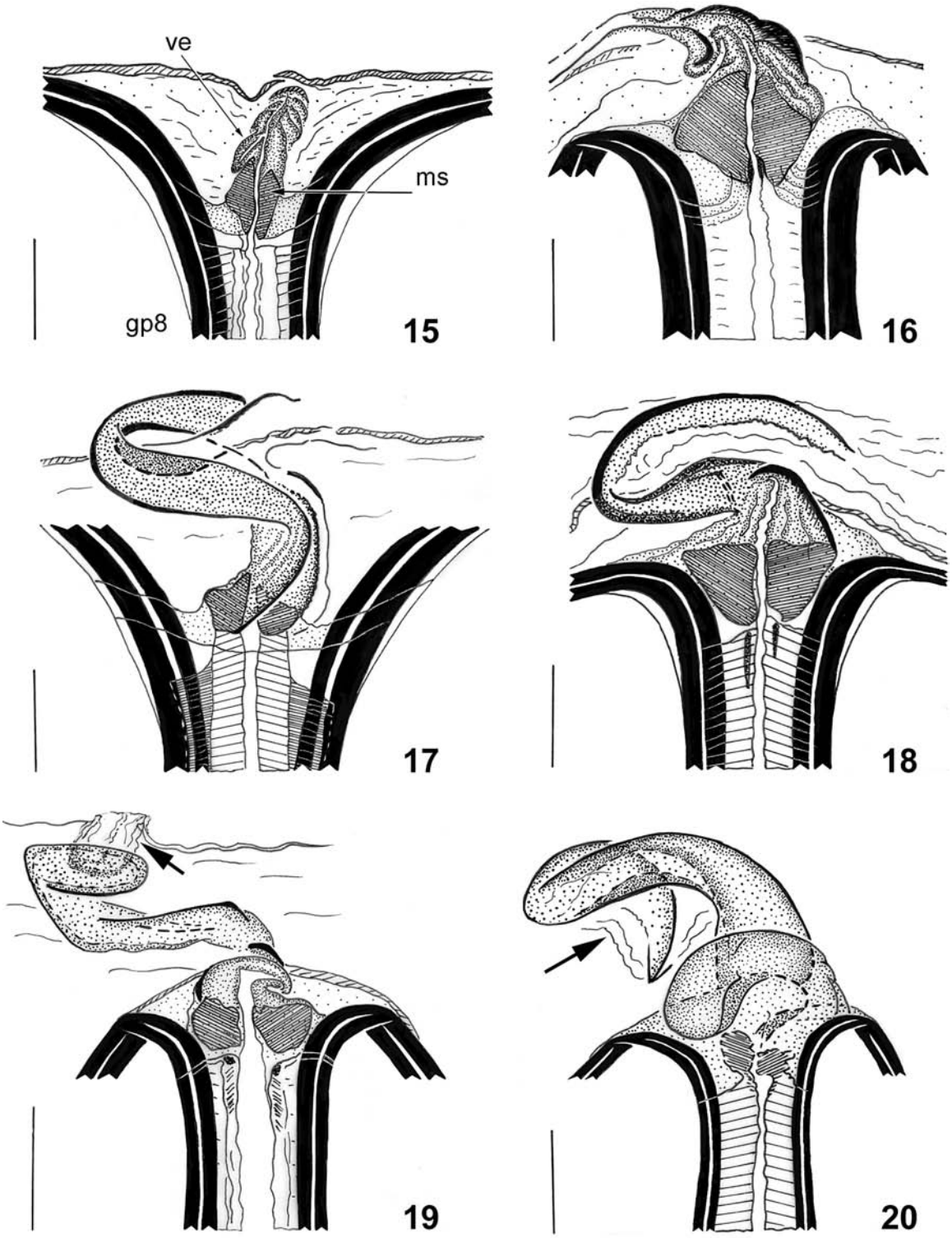


Figs 9-14: Phylinae, base of the ovipositor and vestibulum in various species; the vestibulum is modified into a specialized copulatory duct; (**9**) *Cremnocephalus matocqi* (Hallodapini), general ventral view; (**10**) idem, details of the vesicular diverticle (ventral sac) in lateral view; (**11**) *Anomalocornis peyreti* (Phylini), ventral view; (**12**) idem, detail of the vestibulum; (**13**) *Atractotomus magnicornis* (Phylini), ventral view; (**14**) *Atractotomus kolenati* (Phylini), ventral view; gp, gonapophyses; ov, ovipositor; ss, seminal sac; ve, vestibulum; vs, ventral sac.

structures, simple or complex, may be considered as homologous; all involve the vestibulum, which in some genera appears to be a greatly diversified and highly specialized organ.

Adaptive and functional significance

Orthotylinae and Phylinae are not only sister-groups, they also represent the two groups into which the phallus is potentially the most wounding in the entire family (see Wagner 1955; Kerzhner & Konstanti-



Figs 15-20: Phylinae Phylini, sclerotized differentiation in the vulvar area and the vestibulum; in Figs 17-20, the vestibulum is changed into a copulatory duct strongly sclerotized; (**15**) *Criocoris sulcicornis*; (**16**) *Tuponia macedonica*; (**17**) *Heterocapillus tigripes*; (**18**) *Plagiognathus arbustorum*; (**19**) *Phoenicocoris dissimilis*; (**20**) *Anomalocornis peyreti*; gp8, gonapophyse 8; ms, microsclerite; ve, vestibulum; arrow indicates the connection between the vestibulum and the vagina. Scale bars = 0.1 mm.

NOV 1999; KONSTANTINOV 2003). In our opinion, this observation is certainly significant (although many Mirinae and Deraeocorinae also have potentially wounding vesica, Schwartz pers. comm.).

It is clear that the tendency towards sclerotizations of the vulva and the vestibulum, shared by both Orthotylinae and Phylinae, is highly adaptive and closely related to the male organ. Indeed, in the male, this trend corresponds to sclerotization of some part of the phallus (see WAGNER 1955; SCHUH 1974; KERZHNER & KONSTANTINOV 1999; KONSTANTINOV 2003): – in Phylinae, the sclerotized vesica is long and curved, thin and sharp, usually C- or S-shaped,

sometime looped; – in Orthotylinae Orthotylini, the vesica is short and membranous but the conjunctiva bears several long sclerotized variously branched or toothed appendages. On the other hand, when female genitalia are symmetrical without particular sclerotization, as in Orthotylinae Halticini, the phallus lacks a vesica, the endosoma being membranous with relatively little sclerotized armament.

Moreover, in Phylinae there is a strong correlation between the shape and length of the vestibulum and of the vesica. Such correlation between the male organ and the sclerotized structure of the vestibulum has also been suggested by MAGNIEN (2000) and EYLES & SCHUH (2003). Examples of such correlation are numerous and illustrative: a vestibulum with local C- or S-shaped sclerotized parts corresponds to a C- or S-shaped vesica; the longer and more contorted the vesica, the longer and more contorted the vestibulum; to a duct-like vestibulum more or less looped corresponds a long vesica with complete loop. In *Cremnocephalus*, the length of the looped vesica is correlated with the size of the ventral sac (MAGNIEN, loc. cit.).

Several functions may be attributed to the form of the female structures.

– **Strengthening device for coupling**. It has already been suggested that the sclerotized structures found in the females play a role during copulation, providing a place for attachment of the male copulatory organ during mating (DAVIS 1955), or as a guide and support for the long and looped phallus (EYLES & SCHUH, 2003). Indeed, there is strong evidence for this. According to KERZHNER & KONSTANTINOV (1999), anchoring of the phyline aedeagus in the female genitalia is carried out by the C and S-form vesica. We can add that the anchoring is more efficient if the form of the vesica and that of vestibulum are strongly correlated.

KERZHNER & KONSTANTINOV (1999) and KONSTANTINOV (2003) have shown that in the inflated orthotyline aedeagus some of the sclerotized appendages (processes or spiculi) occupy a position perpendicular to the vesica, apparently acting as an anchor in the female duct. In fact, within Orthotylinae, it seems that during mating the strengthening mechanism is also realized by the very complicated parameres, both being of large size. We believe that they are locked, anchored at several places wedged into the grooved surface of the sclerotized lobes differentiated in the vulvar area. In several orthotyline species, KULLENBERG (1947) recognised the important active part played by the paramere during the first phase to the coupling. He suggested that the sclerotized lobes between the gonapophyses are a strengthening device in *Orthotylus*; *Cyllecoris*-type parameres are used for grasping and holding the pair together and also to disengage the coupling.

– **Defence system for the female**. The sclerotization in the wall of the phyline vestibulum strongly resembles a defence mechanism which reinforces the integumentary area where the male copulatory organ penetrates. The structure guides the potentially wounding vesica to prevent local damage to the genital wall of the female. In Phylinae Phylini and Hallodapini, where the vesica may be very long and coiled with a complete loop, the female genital parts into which the vesica penetrates during copulation may be subjected to great mechanical stress. This justifies a thick intima, and the presence in places of a well sclerotized fold, groove or gutter. The same is true in Orthotylinae where the sclerotized lobes can protect the vulvar area against impact or the huge processes of the parameres.

Within Phylinae, the vestibulum may become a highly specialized organ acting as a copulatory duct. An interesting parallel can be drawn with traumatic insemination in the Cimicidae and Anthocoridae (CARAYON 1966, 1977). When we discovered the strongly pigmented tube-like structure in *Cyllecoris ernsti*, our first thought was that we were looking at a structure strongly reminiscent of the ectospermalege found in the two cimicomorphan groups. Moreover according to CARAYON (1984), in *Pachytomella passerinii* (COSTA) (Orthotylinae Halticini) there is a deep tubular cavity in the vaginal wall which seems house the male long phallic spicule during copulation. We did not find this tubular cavity in the *Pachytomella* species examined (*P. parallela*),

nor any of the various injuries (copulation scars) discovered by CARAYON (1984) in the vaginal wall of several mirid species. Nevertheless, the fact remains that the sclerotized ectospermalege is a defensive response of the integument.

Recently, TATARNIC et al. (2005) reported the existence of traumatic insemination in several species of *Coridromius* (Orthotylinae Halticini). The genus seems involved by a highly accomplished form of traumatic insemination since the site of copulation (spermalege) is localized laterally on the right side of the first visible abdominal segment. This remarkable discovery requires further study.

– **A copulatory tube allowing a direct insemination**? The morphology of the vestibulum may have an important influence on the manner in which sperm is deposited and dispersed. In Miridae, according to KULLENBERG (1947) and CARAYON (1984), the seminal sac (seminal depository) receives the sperm during copulation and most of the sperm migrates and is stored in the pedicel. The sclerotized tube-like vestibulum could be an efficient means for depositing sperm directly into the seminal sac without penetrating the vagina or only slightly. As already remarked, the membranous connection between vestibulum and vagina is particularly difficult to see. Nevertheless, when visible, the connection was realized in the vaginal wall below the right ring sclerite wall and very near of the junction of the seminal sac. When the vesica is inserted into the vestibulum it probably does not enter the genital chamber.

To conclude we remind that the vestibulum has dual functions: in mating and egg-laying. So even though strongly sclerotized and highly modified to form a narrow twisted copulatory tube, the vestibulum retains the ability to stretch to allow the eggs to pass. That can be done since the sclerotized parts of the wall are restricted to longitudinal strips, the other parts of the vestibulum remaining membranous, soft, and much folded.

Acknowledgements

We are grateful to F. Chérot (Université libre de Bruxelles) for discussion and helpful comments on the first draft of the manuscript, and to M.D. Schwartz (Canadian National Collection of Insects, Agriculture and Agri-Food Canada, Ottawa) for many corrections and useful suggestions on a previous version. Thanks are also due to L.A. Costa (Museu nacional, Rio de Janeiro) and G. Couturier (IRD, MNHN, Paris) for kindly providing specimens of *Anomalocornis*, to B. Nau (Dunstable, U.K.) for correcting the English language; and to J. Legrand and Cl. Pierre (MNHN, Paris) for technical assistance with the illustrations.

Zusammenfassung

Die Auswertung von Literaturangaben und neue Beobachtungen zu den weiblichen Genitalien der Miriden zeigen, dass asymmetrische sklerotisierte Strukturen in vier Triben aus zwei Unterfamilien vorkommen: Orthotylinae Orthotylini und Phylinae Hallodapini, Leucophotopterini, Phylini. Diese Strukturen befinden sich in Nähe der Vulva (Orthotylinae) und des Vestibulums (Phylinae). Im letzteren Fall sind die sklerotisierten Strukturen nach rechts gerichtet. Bei den Orthotylinae kann die Vulva von komplizierten Platten oder Loben, die vom inneren Rand der vorderen Gonapophysen (erste Valvulae) entspringen, umgeben sein. Bei den Phylinae kann das Vestibulum durch mehr oder weniger starke Sklerotisierung der Wände stark modifiziert sein. Bei manchen Hallodapini (wenn nicht bei allen) besitzt das sklerotisierte Vestibulum einen blasenförmigen, sackartigen Divertikel. Die sklerotisierten Strukturen scheinen hoch entwickelt und an die Strukturen der Vesika (bei den Phylinae), der Parameren und möglicherweise auch der unterschiedlichen Spikuli der Konjunktiva (bei den Orthotylinae) angepasst. Bei den Phylinae sind Größe und Gestalt der sklerotisierten Teile des Vestibulum an Größe und Gestalt der Vesika angepasst. Daher kann das Vestibulum, wie die Vesika, entweder kurz und gestreckt oder C- oder S-förmig sein, verdreht mit einer Umdrehung oder nicht. In manchen Fällen ist das Vestibulum zu einem hoch spezialisierten Organ modifiziert, dass

als verstärkter Kopulationsschlauch dient. Die hypothetischen Funktionen dieser sklerotisierten Strukturen sind: Verteidigung des Weibchens gegen Verletzungen durch das Männchen; eine richtungsgebende, unterstützende Verstärkungseinrichtung der Vesica bei der Kopula.

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